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BY

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The Pit-closing Membrane in the Wood of the Lower Gymnosperms

By MISS J. G. WRIGHT

(Communicated by R. B. THOMSON, F.R.S.C.)

The attention of the earliest investigators of plant anatomy was drawn naturally to one of the most conspicuous features of the wood elements, the bordered pits. The pit-closing membrane, as an integral part of the pit, received some share of this attention. The pits were studied first in the conifers and were interpreted, according to SANIO (1873), in various ways, by MALPIGHI, LEEUWENHOEK, MOLDENHAWER, KIESER and others. It was not until 1859 that the conception of the bordered pit acquired its present form. In a publication of that year SCHACHT interpreted the borders, not as a modification of the primary membrane, but as folds of the secondary thickening of the wall, with the primary wall running between, dividing the lens-shaped cavity formed by them. This view differed apparently from VALENTIN'S which was put forth unheeded in 1836, only in this respect, that whereas, according to SCHACHT the membrane disappears in the mature condition through resorption, according to VALENTIN it remains intact through its entire life history. SANIO'S discovery of the torus in *Pinus sylvestris* in 1873 settled the question for the pines at least, temporarily. BAILEY (1916) has since shown that in certain conifers the membrane, while thickened centrally to form a torus, shows radiating perforations outside this area. In the case of the cycads, however, opinion regarding the presence or absence of a membrane apparently still wavers as it has done since the early days of research on these forms.

THE CYCADS

BRONGNIART, who first clearly distinguished the cycads from monocotyledons of the palm type, in 1829 declared without hesitation that both cycads and conifers were vessel-less. A few years later, a direct contradiction of this statement appeared in the works of VON MOHL (1832), who considered that while the pits of the side wall have a delicate membrane the end walls must be open because there is a gradual transition from the spiral "vessels" to the pitted ones. Hence, in his view, the latter have been derived from the former and

are, therefore, open. The peculiar point about von Mohl's view with regard to the pits of the side walls is that he considered the membrane to be, not a single median one, but two separate ones, outlining the cavity of the pit and closing both pores. Hartig (1837, 1843) at first emphasized the open condition of the pores but later came to the conclusion that they were to be regarded as open on one side of the pit and closed on the other, *i.e.*, that they possessed a membrane which very frequently was over at one side of the pit, closing one pore completely and leaving the other open. While Schacht (1856) held, as already stated, that the membrane in the pits of tracheids with bordered pits was resorbed, the spiral elements in cycads he considered closed. Curiously enough he did not consider the latter conception to hold for the ferns, for he definitely regarded as vessels the scalariform elements of this group.

According to Mettenius (1861), both Brongniart and von Mohl later agreed that the elements of cycads and conifers are intermediate between vessels and tracheids, as we use the terms, or the vessels and wood cells of the early investigators, since they resemble the former in their pitting and the latter in the fact that they are pointed and closed. The view of Mettenius himself was that in both cryptogams and cycads we find no vessels but only elements with closed ends, whether spiral, scalariform, or pitted. As this conclusion was drawn from a study of macerations it is extremely doubtful whether Mettenius actually saw the pit-closing membrane. His main point was, however, that the wood elements are not made up of a number of superposed cells fused end to end, as he had originally thought, and, hence, are not vessels. Gregor Kraus (1866) also, in his work on the leaves of cycads, based a similar opinion more or less on the shapes of cells rather than on the presence or absence of a membrane[1].

From this time on the cycads were generally regarded as possessing only tracheids. This view was strengthened, doubtless, by Sanio's decisive work on the pines. DeBary in 1884, Engler and Prantl in 1889, Worsdell in 1896, and Scott in 1897, in describing the cycads made mention only of "tracheids." The chief dissenting voice was that of Gwynne-Vaughan (1908) who, in his paper, "On the Real Nature of the Tracheae in Ferns" concluded that true perforations occur in the membrane of some of the cycads, and probably also

[1]One experiences some difficulty in following the thread of early opinion because of the fact that the writers of the period did not distinguish definitely between the elements of primary and secondary growth.

in *Araucaria,* as well as in that of the ferns. This interpretation received support from THOMSON (1913) in his work on the anatomy of the Araucarineae.

The cycads studied in the course of this investigation include both plants with unarmoured, tuberous stems and those of armoured, columnar type. The former are represented in my work by the genera *Stangeria* and *Zamia,* the latter by *Cycas* and *Dioon.*

STANGERIA

The African form *Stangeria paradoxa,* a comparatively small plant with a tuberous underground stem, is in general appearance the most fern-like of the cycads. In wood structure also it recalls the ferns. Text Fig. 2, from the cone axis, and Fig. 1, Pl. I, of the petiole, show the scalariform thickening of the tracheids found typically

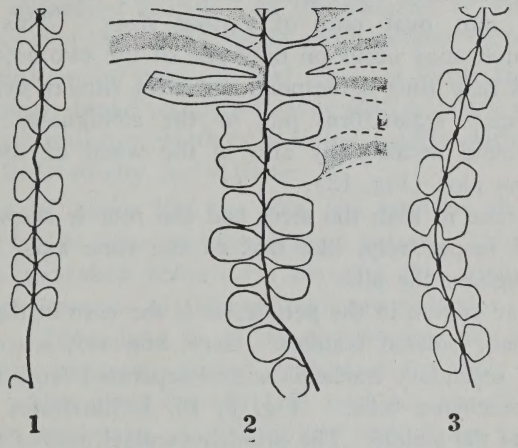


Fig. 1. *Strangeria paradoxa.* Radial section of secondary wood of stem. x 1250.
Fig. 2. *Stangeria paradoxa.* Tangential section of the cone axis. x 1250.
Fig. 3. *Stangeria paradoxa.* Tangential section of root. x 1250.

throughout both the metaxylem and secondary wood of the plant. The bars of thickening extend commonly right across the tracheid or may anastomose with one another producing the oval pits and reticulate appearance of part of Fig. 1, Pl. I. As in the ferns the pitting is not confined to the radial walls but extends completely around the tracheids. In transverse section, the secondary walls seem

to be separated from one another apparently leaving on both sides of the membrane spaces similar to those found in ferns of the *Osmunda* type.

In the vascular bundles of the cone axis very little secondary wood is developed. This is scarcely distinguishable from the metaxylem of the primary. Fig. 2 depicts the latter and demonstrates in the pits a continuous membrane uniform in thickness.

A cross section of the stem, on the other hand, shows numerous radiating bands of secondary wood separated by medullary rays from one to many times their width. The tracheids, however, exhibit very little specialization. The scalariform thickenings are closer together and more frequently united by diagonal branches than in the cone axis and, as seen in section (Fig. 1), form somewhat broader borders to the pits.

The metaxylic and secondary wood of the root resemble that of the stem. Occasionally the regular and closely set scalariform pits are converted into oval ones of various sizes. This formation, peculiarly enough, may occur on only one of the two adjacent walls. Such oval pits may thus correspond not with similar oval ones but with the ordinary scalariform pits of the contiguous wall. This condition is found occasionally also in the wood of the stem and the reproductive axis (Fig. 12).

The membrane in both the stem and the root is shown to be, in Figs. 1 and 3 respectively, like that of the cone axis, of uniform thickness throughout the pit.

The vascular system in the petiole, as is the case in the cone axis, consists of small, isolated bundles. Here, however, a comparatively large group of secondary tracheids occurs separated from the primary by a few parenchyma cells. Fig. 1, Pl. I, illustrates the pitting characteristic of the petiole. The primitive scalariform of the tracheid at the left gives place occasionally to the reticulate arrangement of the secondary thickening seen immediately to the right of the centre. The latter represents the most advanced type occurring in *Stangeria paradoxa*. The membrane in these pits shows no local thickening. In the section photographed it was not stained sufficiently to show clearly.

Although CHAMBERLAIN recognizes only one species of *Stangeria*, viz.—*S. paradoxa*, two lots of material of the petiole which were obtained through the kindness of the Director of Kew Gardens under the specific name *schizodon* both differ in structural detail from the petiole of *S. paradoxa*. In *S. schizodon* the bundles are entirely of

primary origin. A large group of centripetal metaxylem is separated from the protoxylem by a small group of parenchyma cells. In the outer cortex the sclerenchyma cells are much smaller and more fibre-like than in *S. paradoxa*. The pitting also in the form under discussion differs from that of *S. paradoxa*. It is of a more advanced type as shown in Fig. 2, Pl. I, and approaches that of the genera *Cycas* and *Dioon*. In it we find very little open, ring-like scalariform, but chiefly oval pits either uniseriate or multiseriate in arrangement. Fairly numerous also are tracheids like the central one in Fig. 2, Pl. I, with a single row of almost round, broad-bordered pits with slit-like pores.

Zamia

The other tuberous form studied is *Zamia integrifolia*. A transverse section of the stem shows, like that of *Stangeria*, a large starch-filled pith and cortex very incompletely separated by a circle of bundles of secondary growth. In the material of *Zamia* examined there is less wood than in *Stangeria* and a greater proportion of bast.

The pitting in the stem and leaf trace, as illustrated in Fig. 4, is of a close, fairly broad scalariform type with a membrane of medium thickness and uniform width. It stains readily with haematoxylin and shows little affinity for safranin.

The root of Zamia like the root and stem of all the cycads is remarkable for its loose parenchymatous nature. The typical pitting is generally unbroken scalariform merging into broken scalariform through the presence of oblique and perpendicular bridges. The multiseriate pitting here is of two types—that in which the pit borders form an open lattice work, and the type, occurring less frequently, which gives the effect of oval pits embedded in a solid wall. The latter type as well as the scalariform is illustrated in Fig. 5. The membrane which may be either lignified or unlignified is straight, fine, and uniform in thickness.

In the bundles of the leaf the bast is arranged radially, the wood either radially or irregularly. As in the stem several kinds of pitting occur,—chiefly different types of scalariform with, occasionally, examples of the *Cycas* type—round, broad-bordered, with slit-like pores. The membrane, illustrated in Fig. 6 traversing narrow-bordered scalariform pits, shows uniformity of thickness throughout its course.

In the petiole of *Zamia integrifolia* the elements of the protoxylem, the metaxylem, and the secondary wood when present, are, on the

whole, scalariform, with some pitted individuals. In the latter type the slit-like pores are particularly broad and oblique. The membrane shows the typical cycad character.

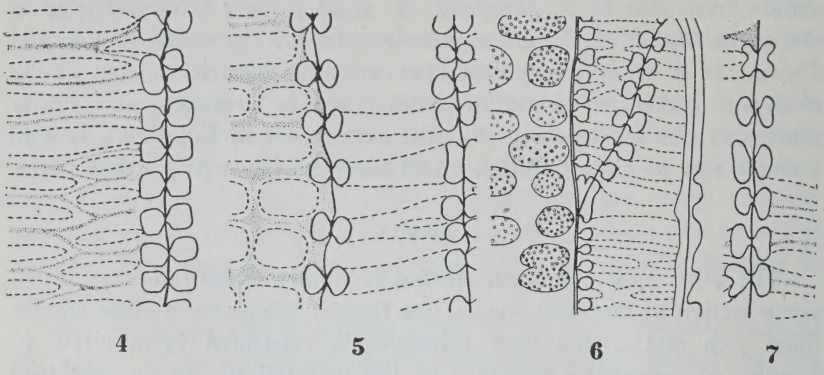


Fig. 4. *Zamia integrifolia.* Radial section of stem. x 1250.
Fig. 5. *Zamia integrifolia.* Longitudinal section of a trace in the region of the hypocotyl. x 1250.
Fig. 6. *Zamia integrifolia.* Radial section of leaf. x 1250.
Fig. 7. *Zamia integrifolia.* Radial section of female sporophyll. x 1250.

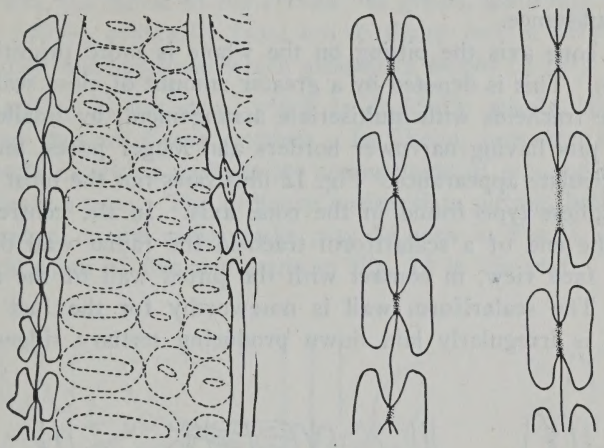
The reproductive parts examined include the female cone axis and sporophyll. In a transverse section of the axis the pith and cortex are practically continuous, hardly broken by a ring of tiny bundles showing secondary growth.

In the sporophyll, illustrated in Fig. 7, there occurs a great deal of ringed and spiral pitting with scalariform of several types. In the figure is shown the most advanced condition approaching the oval type. The membrane appears as a fine dark line closing the pits of adjacent tracheids.

Cycas

In the stem of *Cycas revoluta,* a columnar form, we find a greater amount of wood than in the tuberous forms already discussed. This arises often from more than a single cambium, forming a number of concentric cylinders. The tracheids of the secondary wood possess a type of pitting more advanced than that of either *Zamia* or *Stangeria.* It varies, as described by Sifton (1920) from a type with multiseriate, often flattened pits, to that with uniseriate, and even scattered ones—the result of elimination. The section of the stem

illustrated in Fig. 8 represents a type intermediate between the most primitive and the most advanced. Here may be seen both long oval, and round, occasionally flattened pits. The multiseriate arrangement and the slit-like transverse or slightly oblique pores are evident also. The association here apparent of radial and tangential pitting is typical only of the ends of tracheids. Elsewhere, especially in the later-formed wood, the pitting is practically confined to the radial walls. In the pits cut in section on the left of the figure the uniformly unthickened membrane is apparent, a condition found to be characteristic of *C. revoluta.*



8 9 10

Fig. 8. *Cycas revoluta.* Radial section of stem. x 800.
Fig. 9. *Cycas revoluta.* Tangential section of root. x *ca.* 1500.
Fig. 10. *Cycas revoluta.* Tangential section of petiole. x *ca.* 1500.

I find this type of membrane also present in the stem of another species, *C. media,* although an illustration in a paper by MILLER (1919), on the "Polyxylic Stem of *Cycas media*" depicts the membrane in one of the outer cylinders of this species with a pronounced dot-like torus. As the author makes no reference in the text to its presence, it may be regarded as a conventional touch emphasizing the secondary nature of the tracheids.

As in the case of the stem, the root of *Cycas revoluta* contains a large amount of parenchyma, medullary rays occurring between every two or three rows of tracheids. The pitting of the latter is practically

identical with that in the stem, as is also the pit-closing membrane (Fig. 9).

The pitting in the bundles of the petiole which contain little if any secondary wood includes the usual scalariform varieties and the broad-bordered type. The pits of the latter type are round, two- or three-seriate, smaller and less crowded than those of the stem and root. Their delicate, closing membrane is depicted in Fig. 10. Within the tracheid wall it becomes almost indistinguishable, apparently through partial lignification. With a double stain of haematoxylin and safranin it appears darker red than the secondary wall, due to the obstruction of light by its deeply staining pectin and cellulose substance.

In the cone axis the pitting on the whole is more primitive than in the stem. This is denoted by a greater amount of close scalariform and, in the tracheids with multiseriate arrangement, by smaller, more numerous pits having narrower borders and longer pores, and hence a more reticulate appearance. Fig. 12 illustrates not the most general, but the highest type found in the cone axis. In the centre of the figure is the end of a scalariform tracheid the radial wall of which is seen in face view, in contact with the pitted wall of the adjacent tracheid. The scalariform wall is noteworthy for the fact that its thickening is irregularly laid down producing tertiary ridges on its

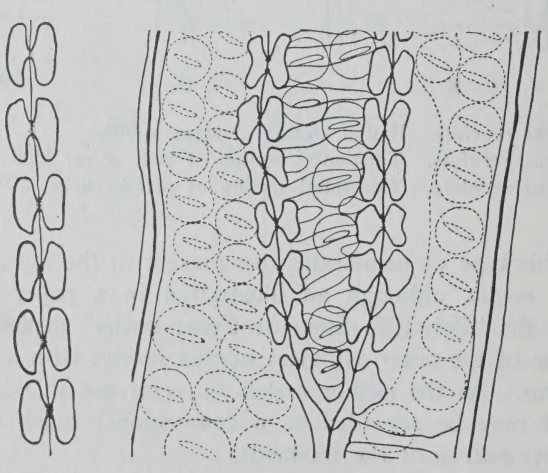


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Fig. 11. *Cycas sp.* Tangential section of seedling root. x 800.
Fig. 12. *Cycas revoluta.* Radial section of reproductive axis. x 800.

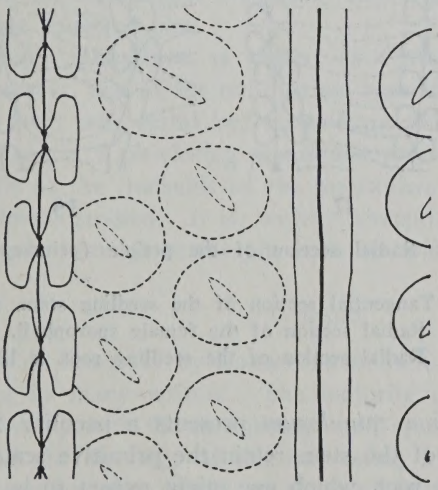
bars. The ordinary type of pitting on the radial walls is indicated in dotted outline on the tracheids at the sides. The pits on the cut walls show the unthickened membrane so characteristic of the cycads.

The seedling root and hypocotyl present a fairly close resemblance in their pitting to the petiole, described above. The pits of the seedling root have been illustrated in section only (Fig. 11) and are seen to be traversed by the typical cycad membrane.

DIOON

Dioon spinulosum is, with the exception of *Macrozamia Hopei* of Australia, the tallest of the cycads. It grows, according to CHAMBERLAIN (1919) ordinarily from ten to thirty feet in height, but he has recorded one specimen which attained a height of fifty feet.

The pitting in the stem, which is decidedly woody, differs very little from that of *Cycas revoluta.* In *Dioon,* however, are found fewer tracheids with a multiseriate arrangement of pits and more with the elimination type. The ordinary multiseriate pitting, both opposite and alternate, of the radial walls may be seen in Fig. 3, Pl. I, and the typical form of the membrane in Fig. 14 in the text.



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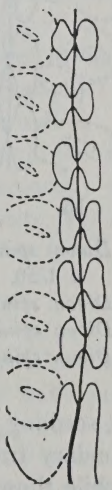

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Fig. 13. *Dioon spinulosum.* Tangential section of the root. x 1250.
Fig. 14. *Dioon spinulosum.* Tangential section of the stem showing the presence of a membrane in the end wall of a tracheid. x 800.

The wood of both the root and the petiole of this form is so similar to that of the corresponding regions of *Cycas revoluta* that a separate description is not necessary. The pits of the root with their closing membrane are illustrated in both radial and tangential view in Fig. 13, those of the petiole in Fig. 15.

In the sporophyll bundles there are a few elements of wood, adjacent to the radially arranged bast cells, which may be of secondary origin. It is very doubtful, however, whether this is the case especially as the pitting is entirely of ringed, spiral, and open scalariform type (Fig. 17). The membrane, here again, is seen to be characteristically delicate and uniform in thickness.

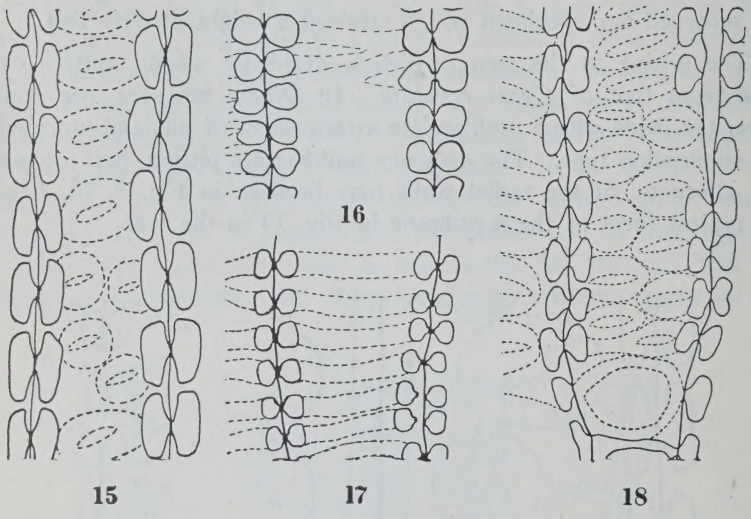


Fig. 15. *Dioon spinulosum.* Radial section of the petiole (primary wood). x 1250.
Fig. 16. *Dioon spinulosm.* Tangential section of the seedling stem. x 1250.
Fig. 17. *Dioon spinulosum.* Radial section of the female sporophyll. x 1250.
Fig. 18. *Dioon spinulosum.* Radial section of the seedling root. x 1250.

The seedling of *Dioon spinulosum* presents a peculiar feature. The secondary tracheids of the stem retain the primitive scalariform pitting while those of the root, which one might expect to be especially primitive in character, develop the more advanced multiseriate pitting characteristic of *Cycas* and *Dioon*. Figs. 16 and 18 bring out this difference. The root (Fig. 18) is seen to resemble that of the adult. In the seedling, however, there is a decrease in size of

tracheids and pits. The latter, too, are more oval with longer pores. The membrane shows no peculiarity but is continuous and unthickened in both regions (Figs. 16 and 18).

It is of interest to note in conclusion that in *Dioon* as well as in all the other cycads examined the terminal pitting whether on the tangential or radial wall has a distinct membrane (cf. Figs. 8, 12 and 14) and that in no case is the membrane missing as in certain ferns (DEBARY, 1884; HIRASE, 1897; WRIGHT, 1920).

SUMMARY OF THE CYCADS

1. The wood of *Stangeria paradoxa* consists of scalariform tracheids of various types in addition to ringed and spiral elements.

2. In the petiole of *Stangeria schizodon,* besides elements similar to those of *S. paradoxa,* there occur tracheids with round, broad-bordered pits having long, oblique pores.

3. The wood of *Zamia integrifolia* resembles that of *Stangeria paradoxa.*

4. In *Cycas revoluta* the multiseriate type of pitting is attained. The pits, in face view, are round, broad-bordered, with oval, transverse or oblique pores. There is a preponderance of multiseriate pitting in all regions but frequently this type gives place to bi- and uni-seriate scattered pits.

5. *Dioon spinulosum* is similar to *Cycas revoluta* in its pitting with, however, less of the multiseriate type. In the sporophyll and the seedling stem only spiral and scalariform pits are found.

6. There is a pit-closing membrane present in both the side and end walls of the tracheids of the metaxylem and secondary wood in all the forms studied. It is, without exception, delicate and uniform in thickness throughout the pit, with no evidence of a torus.

GINKGO

Since its discovery by KAEMPFER in 1690, *Ginkgo biloba* has been discussed by many writers. The majority of these have been concerned mainly with the morphology and systematic position and very little with the histology of this interesting form. The most comprehensive and complete works are those of SEWARD and GOWAN (1900) and of SPRECHER (1907). These authors give excellent historical sketches and bibliographies to which the reader is referred.

On morphological grounds, according to SPRECHER, the genus has at different times been variously placed in systems of classifica-

tion. Beginning with a position close to *Taxus,* in 1796, it has made the circuit through the *"Monoecia polyandria"* (between the genera *Corylus* and *Platanus*) and the Amentaceae back to the Taxaceae again, where it remained practically until the beginning of the present century. From an anatomical point of view the relationship of *Ginkgo* has generally been conceded to be with the *Taxus* group. The work of HIRASÉ (1897, 1898), of SEWARD and GOWAN (1900), and of SPRECHER (1907), among others, has finally accorded the Ginkgoales the dignity of a phylum separate from that of the Coniferae and intermediate between the latter and the Cycadales.

Practically no work has been recorded on the pit-closing membrane in *Ginkgo* but the pitting has been the subject of many descriptions. The primary wood and the transition area between primary and secondary seem to have been particularly striking. It was from this region that VON MOHL illustrated his theory of the development of pitted tracheids from "spiral vessels." The latter he found particularly large and abundantly developed. DIPPEL (1862) and BERTRAND (1874) also described this region. Judging from the structure of the mature wood as well, GOEPPERT (1850, 1883) classed the genus with the Taxineae. From his illustration of a radial section it is evident that this author followed VON MOHL in regarding the pit as closed by two lateral membranes instead of a median one. In 1891 STRASBURGER described an old stem, fifty-eight years of age, but added little to our knowledge of the pitting or membrane. SEWARD and GOWAN (1900), on anatomical grounds in addition to the morphological ones already mentioned, advocated the removal of *Ginkgo* from the Taxaceae. This view received the support of GOTHAN (1905) who, however, stressed the araucarian-like structure of the wood. JEFFREY (1917), on the contrary, disclaimed all araucarian or taxinean affinities for *Ginkgo* preferring to regard it as a link between the Archigymnospermae, particularly the Cordaitales, on the one hand, and the Metagymnospermae, notably the Abietineae, on the other.

The most detailed anatomical account is that of SPRECHER (1907) in which is described and figured the wood from all regions. In his figures the membrane is always shown, not only in the sides but also in the end walls of the wood elements both primary and secondary. In describing the former the author speaks of "trachées annelées" and "trachées reticulées" and on p. 67 we find, "Les elements ligneux exterieurs presentent sur leurs faces radiales des ponctuations areolées ce que prouve leur nature tracheidale." Thus

with Sprecher the criterion of a vessel is evidently not the absence of a membrane but the type of pitting.

The regions of Ginkgo studied in this investigation are,—the stem, root, and petiole; the reproductive axis and peduncle; and the hypocotyl, stem, and leaf of the seedling.

The pitting, represented by that of the stem (Fig. 4, Pl. I), combines characters of both araucarians and pines. The round, broad-bordered pits are arranged in one or two rows either opposite or alternating. Close, small bars of Sanio as well as those of the long straight type are prominent in properly stained sections. The pores are large and round. As in the case of the araucarians the pore is apparently continued on either side as a thin area in the pit border. This area, although not an actual opening, gives an elongated, pointed outline to the pore, the two opposed to one another on adjacent walls producing an X effect suggestive of the cycads. This effect is seen in the photograph in the uniseriate tracheid on the left, between two empty ones, and faintly in the centre. In section the walls of the tracheids show certain features different from those in either the cycads or the araucarians. The central region of those parts of the secondary walls, which form the "spools" between the pits, are concave toward the lumen while their ends which form the borders of the pits become thin and bowed in that direction. Thus half of each spool, formed by the wall of a single tracheid, suggests the spread wings of a bird (Fig. 23 of the root). This gives the "spools" a more graceful and delicate appearance than those of either of the above groups (Figs. 11, 14, 30, etc.) and produces a larger cavity in proportion to the thickness of the wall.

It is generally true of the wood of *Ginkgo,* as of that of *Cycas,* that the layers of the primary wall on either side of the membrane within the spools are partially lignified. In *Ginkgo* they have been found to separate at the edge of the pit and to follow its inner margin, frequently almost to the pit pore, thus bounding the cavity. This has been illustrated clearly only in Fig. 25, where it was observed most readily because of the absence of stain in the secondary layers of the wall.

The pit-closing membrane in *Ginkgo* has not been described in the literature but has been incidentally figured by SPRECHER (1907) in his work, *"Le Ginkgo biloba".* In his illustrations of an old stem two types of membrane are shown,—one unthickened, the other spindle-shaped in section, but no reference is made to their presence or distribution. In my material of *Ginkgo* also the membrane shows

a dual character. In the stem (Figs. 19 and 20) it is either uniform and delicate or exhibits an elongated, dot-like torus about one-half the length of the pit pore. In the short shoot two types occur also. These are illustrated in Figs. 21 and 22. In Fig. 22 this torus is shown both in section and face view and has a diameter about that of the pit pore. The membrane may be traced as a hair-like line connecting the torus with the primary wall. Occasionally the dot-like torus dwindles off to a spindle the length of the pore.

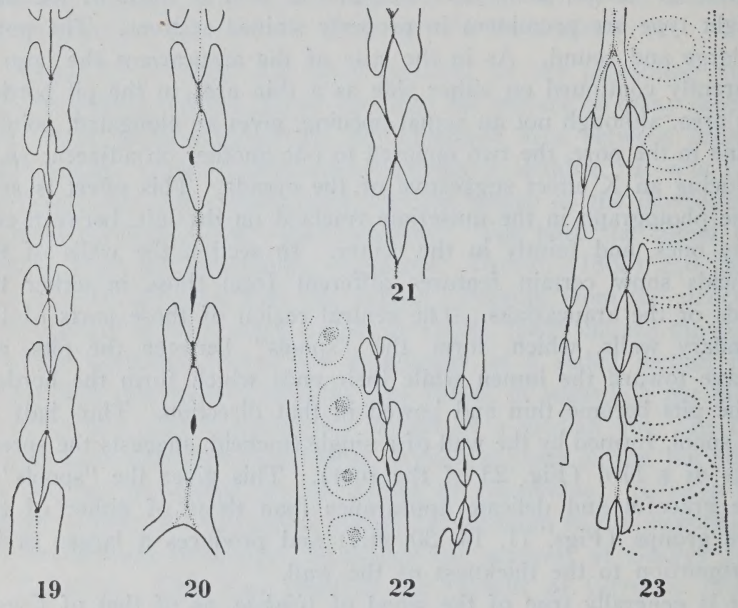


Fig. 19. *Ginkgo biloba.* Tangential section of old stem. x *ca.* 1000.
Fig. 20. *Ginkgo biloba.* Tangential section of old stem near cambium. x *ca.* 1500.
Fig. 21. *Ginkgo biloba.* Tangential section of short shoot. x *ca.* 1500.
Fig. 22. *Ginkgo biloba.* Tangential section of short shoot. x *ca.* 1000.
Fig. 23. *Ginkgo biloba.* Tangential section of the primary wood of the root in the transition area. x *ca.* 1500.

In the root the primary wood was studied as well as the secondary. In the metaxylem of the transitional region of the former the pits are oval rather than round and have narrow borders and large pores (Fig. 23). The membrane in this region is always unthickened or very slightly thickened, in the form of a delicate torus fusiform in section. The drawings shown in Figs. 24 and 25 were made from

sections of the old root stained with ruthenium red, and exhibit the typical membrane in this region. It is straight and thin in the first formed elements of the secondary wood, and through thickening in the middle or thinning at the ends or both, it gradually develops a torus, indefinite at first, thin and spindle-shaped in section, extending slightly beyond the pit pore. Within the tracheid wall the membrane is seen with difficulty owing to lignification.

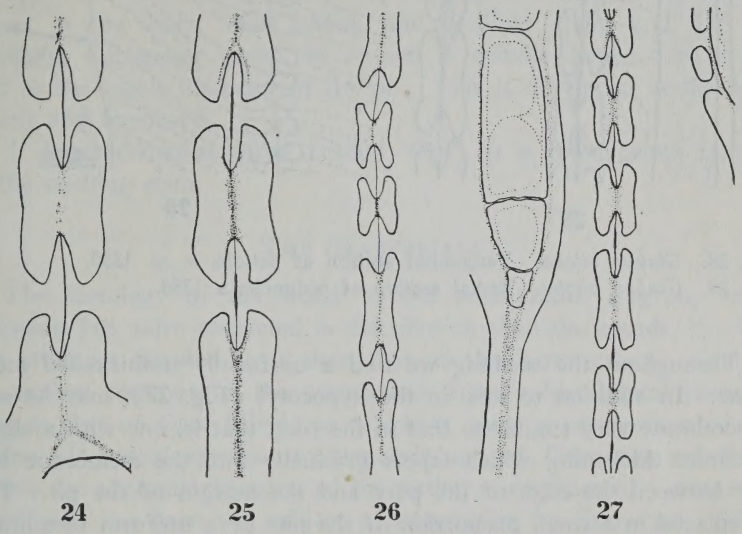
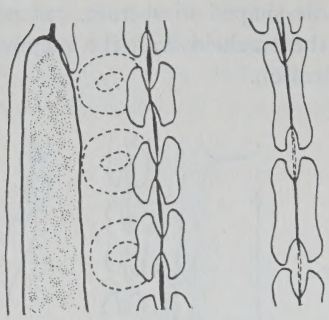


Fig. 24. *Ginkgo biloba.* Tangential section of root. x *ca.* 1500.
Fig. 25. *Ginkgo biloba.* Tangential section of root. x *ca.* 1500.
Fig. 26. *Ginkgo biloba.* Tangential section of seedling stem. x *ca.* 1000.
Fig. 27. *Ginkgo biloba.* Tangential section of hypocotyl. x *ca.* 1500.

Fig. 28 is a drawing of the secondary wood of the petiole. The pitting is shown both in face view and in section. It differs from that of the stem in having oval rather than round pits and pores. There is developed a thin, uniform membrane or a slightly thickened one producing in section a long spindle stretching from end to end of the pit.

Of the reproductive parts examined the peduncle alone is illustrated (Fig. 29). The specimen contained little if any secondary wood. In longitudinal section the tracheids are short, broad and tortuous, and exhibit no pitting of a type higher than that illustrated. The membrane traversing the pits, of the slightly bordered, unbroken

scalariform type, is seen to be continuous and of uniform thickness. That of the spur shoot bearing the ovulate axis is uniform also, although there is much more secondary wood present.



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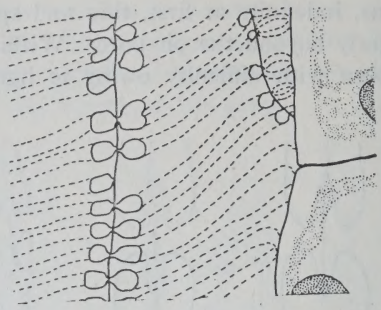

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Fig. 28. *Ginkgo biloba*. Tangential section of petiole. x *ca.* 1250.
Fig. 29. *Ginkgo biloba*. Radial section of peduncle. x 1250.

Throughout the seedling we find a uniformly unthickened membrane. In addition to this, in the hypocotyl (Fig. 27), may be seen a membrane very similar to that in the root, that is, one with a slight, indefinite thickening which tapers gradually into the membrane half way between the edge of the pore and the margin of the pit. This is replaced in a small proportion of the pits by a uniform membrane. The primary wood and the first formed elements of the secondary in the older seedling stem (Fig. 26) again exemplify the uniformity of the pit membrane. Early in the formation of the secondary, however, a torus is developed. It is about the length of the pit pore and taper-pointed like that of the hypocotyl. Farther from the pith thickenings are found as illustrated in Fig. 10, Pl. II. In tangential view this second type resembles that found in the short shoot (Fig. 22). In section it is a very definite, short, filiform torus with a connecting membrane so fine as to be nearly invisible and often torn away. This torus is interesting in face view. It is of the strap-shaped or spider-like type first figured by BAILEY (1916) in *Dacrydium Franklinii*. Fig. 10, Pl. II, shows its central, irregular region tapering off into transverse arms varying in number and size. In the lower pit the rather large, heavily stained central part dwindles on each side into two short arms. In one of the upper ones the arms are delicate and more numerous.

Summary of Ginkgo

1. The pitting of *Ginkgo biloba,* in the stem, root, petiole and seedling attains to the round, broad-bordered type with oval to round pore. The pits are both opposite and alternate in arrangement. The peduncle shows only the bordered scalariform type.

2. A uniformly unthickened pit membrane is found in all regions of Ginkgo. In addition to this, several types of torus occur. These are (1) a small rather definite thickening, disc-shaped in section, found in the stem, short shoot, and seedling stem, and (2) an indefinite thickening which, in section is spindle-shaped and equals half or the whole diameter of the pit. This is developed in the root, petiole and hypocotyl.

3. A strap-shaped torus (radial view) is a conspicuous feature of the seedling stem.

The Araucarians

The histology of the wood of the araucarians, a group more abundant but more restricted in distribution than the cycads, has had less attention devoted to it than that of the latter group. One of the earliest treatises on the araucarians from a histological point of view is that of Don (1841) in which is made a comparison of the pitting of several species of *Araucaria* and of *Dammara orientalis.* In this the alternate character of the pitting is emphasized. *Araucaria brasiliensis* has been the subject of description by Schacht (1860) and Winkler (1872). In the case of the latter only is there presented any idea of the construction of the pits of the wood. The illustrations indicate that Winkler considered the pit a cavity in the primary wall for the latter seems to divide and surround the cavity of the pit, closing the pores at both sides and thus leaving no median membrane. However, the statement that pits on tracheids touching the medullary rays are closed next to the latter seems to imply that they may be open elsewhere. His work thus leaves one in doubt as to the closed or open condition of the pit. All of Goeppert's (1850, 1883) illustrations show the closed condition not only in the wood of the araucarians but in that of *Ginkgo,* the pines, etc. In a drawing of *Pinus Larix* one pit only is represented as divided by a fine, median membrane. Evidently Goeppert was not aware of the torus in *Pinus* even at the time of his later publication.

The first suggestion of the presence of a torus in the araucarians is that of Sterzel (1900-1903). He worked with fossil forms and

accounted for the appearance of certain disc-like structures in the wood on this basis. GOTHAN (1905) working over the same material explained the disc effect as due to the outline of the "Steinkern" of the pit at the particular plane at which the section was cut, for he claimed that it was unlikely that the thin torus would be the only part "humifiziert" and hence coloured. A study of living forms was made incidentally by THOMSON (1913) who found a great reduction in the limiting membrane compared with that of the Abietineae. A torus fusiform in section was found to occur occasionally in the pits of the summer wood in the stem. Elsewhere the limiting membrane, which developed at the cambium and persisted for several tracheids inward, disappeared with nowhere a trace of a torus. JEFFREY (1917) observed a torus in the region near the primary wood of the cone axis and nowhere else.

Araucaria Bidwillii, Araucaria imbricata and *Agathis australis* supplied the greater part of the araucarian material for this work. In each species the parts studied include at least the adult stem and root, the cone axis, and various parts of the seedling. The character of araucarian pitting in general may be illustrated by the stem of *Agathis australis,* Fig. 5, Pl. I. The pits which are round to oval have characteristically oval, oblique pores. They are practically confined to the radial walls of the tracheids, occurring chiefly toward their ends. In the photograph the uniseriate to triseriate, alternate arrangements are depicted. The number of rows frequently runs higher, occasionally up to four or five. A feature to be noted is the lack of the so-called characteristic hexagonal outlines of the pits. These are suggested in the third tracheid from the left but are by no means so prevalent in nor so characteristic of the mature wood of the araucarians as is generally held.

ARAUCARIA BIDWILLII

Araucaria Bidwillii, the Bunya Bunya, is a large tree one hundred to one hundred and fifty feet in height with whorled branches on which are borne closely set, sessile leaves three-quarters to one and one-half inches in length. The dense leafy cover is given a very characteristic appearance by the occurrence at intervals of whorls of smaller leaves, the unaltered outer layers of the naked bud. The species is indigenous to Queensland.

The wood of the stem differs slightly from that of *Agathis australis.* The tracheids and pits are of similar dimensions; the pores,

however, are shorter and broader than in *Agathis,* often almost round. Where the tracheid touches a medullary ray in *A. Bidwillii* the pits are larger than the corresponding ones of *Agathis* and have broader pores. The closing membrane of the pit may be uniform in thickness (Fig. 30), or exhibit a peculiar torus (Fig. 31). Fig. 30 demonstrates, in *A. Bidwillii,* as in the cycads, the presence of a membrane in the pits of the end wall. It is difficult to determine the exact boundaries of this torus or, indeed, sometimes even its presence as the pits appear very different under different conditions of light. Fig. 31 shows two different appearances of the membrane in the same row of pits in the stem of *A. Bidwillii.* Fig. 31a is due to the use of a very strong light which penetrates the torus producing a shadow only at its very edge. This gives the effect of a double membrane with space between. Fig. 31b is produced by the use of less light which illuminates both halves of the pit to an equal degree. With such light the torus which has apparently absorbed both haematoxylin and

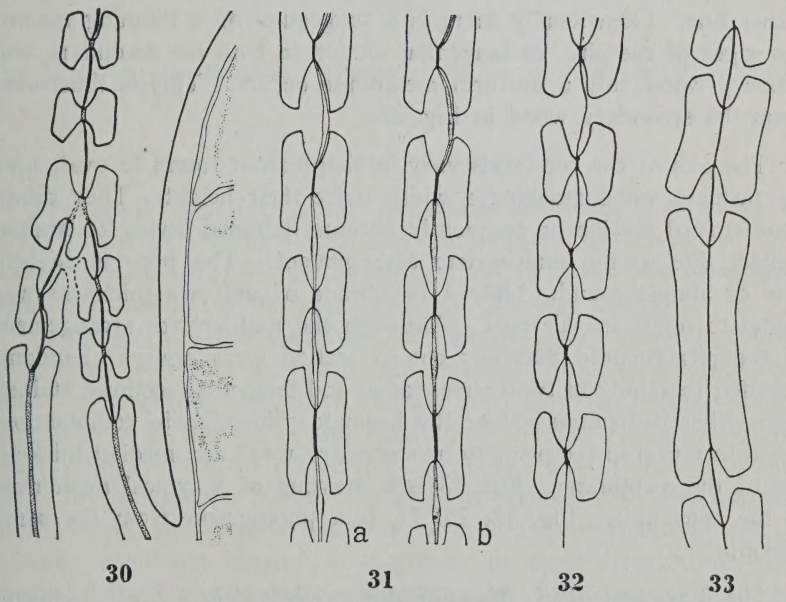

Fig. 30. *Araucaria Bidwillii.* Tangential section of old stem showing the presence of a membrane at the end of a tracheid. x 800.

Fig. 31. *Araucaria Bidwillii.* Tangential section of stem showing different appearances of membrane due to light. x 1250.

Fig. 32. *Araucaria Bidwillii.* Tangential section of root. x 1250.

Fig. 33. *Araucaria Bidwillii.* Radial section of cone axis. x *ca.* 1500.

safranin is pale gray with a tinge of pink bounded by a darker line on either side.

Artefacts of a similar nature are common throughout the forms studied. In the cycads, for example, where the membrane is uniform in thickness and, on the whole, exceedingly clear, there are times when a weak stain gives the effect of a slight thinning toward the edge of the pit. This effect may be due either to an actual absence of stain toward its edge or to a uniform stain and a greater depth of membrane at the centre of the pit. The latter condition would present greater possibilities of folding or other irregularities which might increase its apparent thickness. In support of this interpretation, I may say that I found the artefact more pronounced in the deeper pits.

In the young root of *A. Bidwillii* the tracheids bear more numerous pits than in the stem and the pores are slightly longer and narrower. The membrane as seen in transverse section is uniform in width and rather fine. Occasionally there is a suggestion of a thinning toward the edges of the pit. In tangential section in both the secondary and primary wood only a uniform membrane occurs. This is illustrated from the secondary wood in Fig. 32.

The pits of the cone axis vary in shape from round to oval, near the primary wood reaching a width twice their height. They retain their curved outline or frequently become flattened owing to mutual contact due to the multiseriate arrangement. The pore is slightly oval or almost round. Only a membrane of uniform thickness was found to occur in this part. Although the multiseriate arrangement of the pits ensured that pits cut in section were always abundant, repeated searching in transverse, radial and tangential sections, stained with either ruthenium red or the haematoxylin-safranin combination, failed to reveal in the primary or secondary wood any median thickening of the membrane. Fig. 33 is a drawing of a typical membrane in the cone axis. Fig. 12, Pl. II, is a photograph from the same region.

The hypocotyl of *A. Bidwillii* also exhibits only a fine pit-closing membrane on which no torus has developed. This is evident in transverse section in Fig. 34.

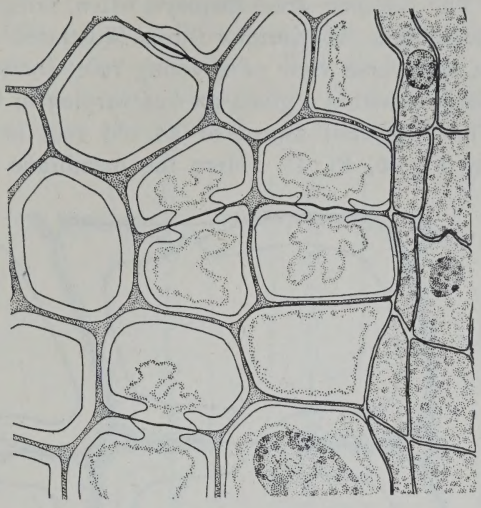

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Fig. 34. *Araucaria Bidwillii.* Transverse section of hypocotyl at cambium. x 1250.

ARAUCARIA IMBRICATA

The South American form, *Araucaria imbricata,* is a native of Chili where it grows to a height of one hundred feet or more. The leaves, spirally crowded, and imbricated, are rigid and very persistent, hence responsible for the common name "Monkey Puzzle."

In the mature stem examined the pits are usually closely grouped in a single row and open into the tracheid through oval, diagonal pores. The closing-membrane of these pits, like that in the younger stem, shows in transverse and longitudinal section a narrow spindle slightly longer than the diameter of the pore. Fig. 35 illustrates this torus in the summer wood. In sections stained with Haidenhain's haematoxylin and safranin the torus is more prominent throughout the summer wood not because of a greater or more frequent development of it at this point as suggested by THOMSON (1913), but because of its greater affinity for haematoxylin. The spindle is quite as consistently present in the spring wood but is very little affected by this stain.

In radial view the ends of the tracheids in the root are seen to possess round, oval-pored pits with an alternate and uniseriate scattered

arrangement. The summer wood displays, often, irregular tangential pitting. The membrane has various forms illustrated in Figs. 36 to 39. Fig. 36, a transverse view of a young root, shows a membrane uniform in thickness within a given pit but varying in thickness from pit to pit. The tangential aspect of an old root is illustrated by Fig. 38 and by Fig. 6, Pl. II. Here the membrane has a definite

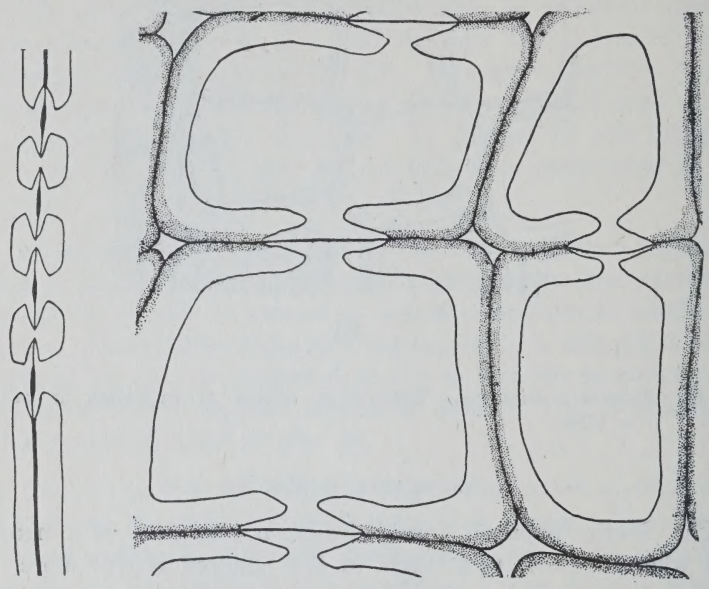

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Fig. 35. *Araucaria imbricata.* Tangential section of summer wood of stem. x 1250.

Fig. 36. *Araucaria imbricata.* Transverse section of young root. x *ca.* 1500.

though delicate spindle slightly longer than the pore. A phenomenon which was found also in *Ginkgo* is illustrated in Fig. 39, and Fig. 9, Pl. II. The membrane, evidently subjected to unwonted strain through sectioning, has split, and the split halves, which exhibit slight thickening opposite the pores, lie in various positions in the pit. In some cases the halves of the common membrane thus pulled apart join the halves of similarly split bars of Sanio above and below the pit.

In *A. imbricata* the pitting of the female cone axis resembles that in the stem and root more closely than in the case of *A. Bidwillii.* The pits are of the usual round, broad-bordered type with an oval,

oblique pore. Where biseriate they are alternate but are very often uniseriate. There is very little tangential pitting although more, perhaps, than in the root and stem. The pit borders in longitudinal section are of the typical "square-jawed" araucarian type. The primary wall is broad and lignified. In this form as in *A. Bidwillii*

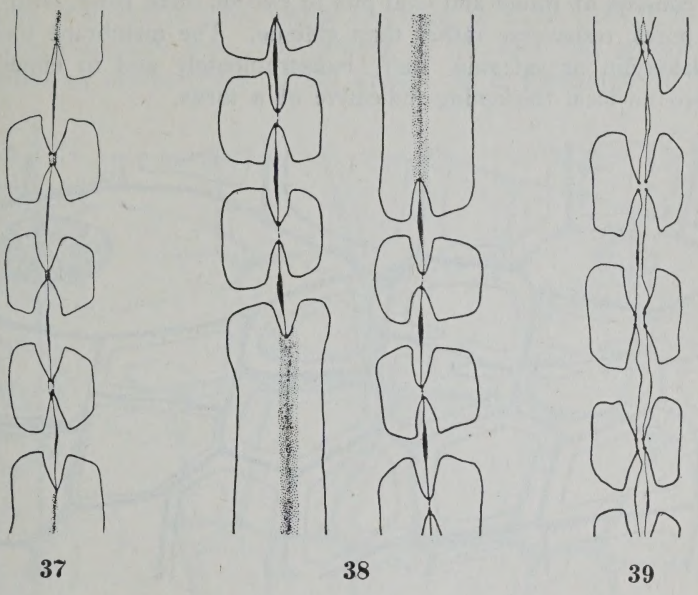

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Fig. 37. *Araucaria imbricata.* Tangential section of old root. x *ca.* 1500.
Fig. 38. *Araucaria imbricata.* Tangential section of old root. x *ca.* 1500.
Fig. 39. *Araucaria imbricata.* Tangential section of the old root showing the membrane split in two. x *ca.* 1500.

no torus could be discovered. In the entire range of pits from primary wood to cambium of the adult cone the membrane was found to be consistently uniform and of medium thickness. Any variation that occurred was toward a uniform thinning of the whole membrane.

The cone axes of two other species, *A. Cunninghamii* and *A. brasiliensis,* were examined also. The results obtained from this region of *A. Cunninghamii* can hardly be compared with those of the other forms as the only material available was a very young cone axis. Here the tracheids, although of secondary origin, are very primitive in character. The thickening of their walls is in the form of fine scalariform bars combined frequently with the very open type of bordered pit so characteristic of transitional xylem of primary

wood. The membrane, too, emphasizes this resemblance to primary wood. In section it is very straight, unthickened, and stains readily with haematoxylin.

In the case of *A. brasiliensis* also the material was quite young with, however, some pitting other than scalariform. The more mature type consists of round and oval pits in two or three rows, with large, oval pores, transverse rather than oblique. The membrane took the haematoxylin or safranin stain indiscriminately and in either case showed no local thickening indicative of a torus.

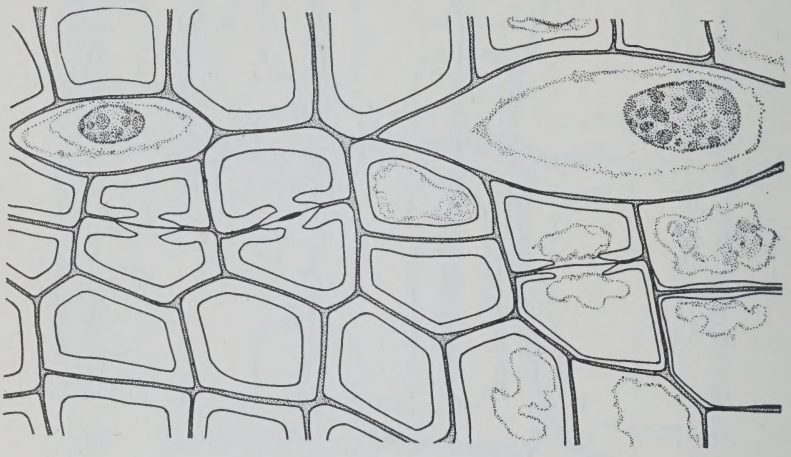

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Fig. 40. *Araucaria imbricata.* Transverse section of the stem of the seedling. x 1250. The membrane in the pit at the left has been moved two tracheids toward the cambium in order td bring it within the area drawn.

The seedling stems of *A. imbricata* examined were young ones containing twelve to fifteen rows of secondary wood. In radial view the tracheids exhibit round, occasionally oval, broad-bordered pits with a round pore. Typically the pits are very close in a single row, often slightly flattened by contact, and usually with a prominent, short bar of Sanio between them. In transverse view the pit-closing membrane is usually uniform in thickness. In a few cases near the cambium there occurs a clear-cut torus (Fig. 40). This is small and in section resembles a flattened spindle. It extends usually beyond the edges of the pore and is connected with the margin of the pit by a fine membrane.

AGATHIS AUSTRALIS

The genus *Agathis* will be illustrated by *Agathis australis,* the "Kauri" of New Zealand. It attains approximately the same height as the two species of *Araucaria* already dealt with. The leaves are oblong, very thick, and obtuse at the apex. In young plants they measure from one to three inches according to KIRK (1889), in older plants considerably less. The pitting of the stem has already been described as characteristic of the group. It is illustrated in Fig. 5,

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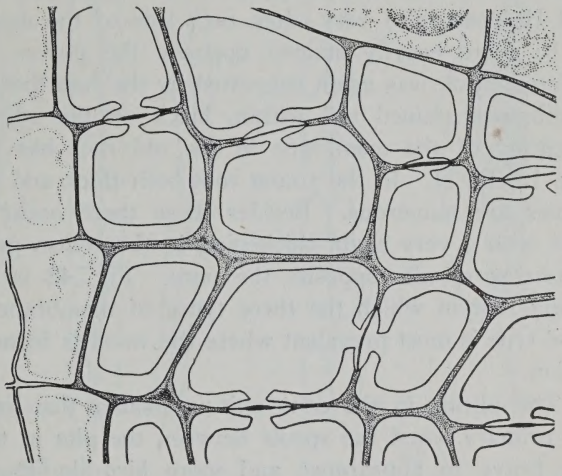

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Fig. 41. *Agathis australis.* Tangential section of the stem. x 1250.
Fig. 42. *Agathis australis.* Transverse section of the cambial region of a young root. x 800. This drawing is a composite one as regards the membrane. All the types found in the region have been collected without alteration in their relative positions.

Pl. I, and the membrane in Fig. 41. This membrane is of medium thickness and typically either uniform in width or slightly thinned at its very margin. *Agathis australis* is perhaps not entirely representative of the genus in this respect, as a cursory examination of two other forms, *A. Moorei* and *A. Bidwillii,* has revealed in this region the occasional presence of the characteristic araucarian torus, spindle-shaped in section.

The tracheids in the root of the material of Kauri examined show a remarkably large diameter reaching an average almost twice that

of those in the stem. The pits in both regions are approximately the same size and so more numerous in the root. Here the pits are seen to be in three or four rows across a tracheid. At the pointed tips this number is reduced to two or one. The distribution of the pits on the tracheid is less restricted than in the stem. From a study of transverse and tangential sections the membrane in the wood of the old root was found to be locally unthickened. Several different stains used all revealed it as a straight line in section either very thick, the thickness of the middle lamella within the walls, or quite fine. When stained with safranin and haematoxylin (both Delafield's and Haidenhain's) very often each side of the membrane was found to be more heavily stained opposite the pores. Possible chemical differentiation was again suggested by the fact that many of the thick membranes stained red within, black on the edges. The typical condition of the membrane in the old root has been illustrated in Fig. 13, Pl. II. In the young root both thick and thin straight membranes are numerous. Besides these there occur sporadically, thin ones with a very slight thickening in the centre producing in section a narrow spindle opposite the pore. Fig. 42 is a drawing of the young root in which the three types of membrane are shown. The third type is most prevalent where the wood is forming, at the cambial region.

The pitting in the cone axis is smaller than in the stem. Near the primary wood the spools between the pits in tangential view are less heavy in appearance and more bird-like than is usual in the araucarians. A number of different stains used here, as in the root, confirmed the view that the membrane in the pits, although lacking a torus, takes more than one form. It develops normally as a thin, or sometimes as a very thick, straight membrane (Figs. 8 and 11, Pl. II).

The tracheids and pits in the seedling stem and root are smaller than in the adult and are comparable with those of the cone axis. The pits in face view are round or oval, with an oval pore which tends to be longer in the root than in the stem. They are disposed in one or two rows, near the primary wood being alternate and biseriate. The membrane in the seedling stem is prevailingly lignified as indicated by its absorption of safranin only from Haidenhain's iron alum haematoxylin-safranin combination. In a two year old stem taken in the fall the pit membrane took the haematoxylin stain only in the summer wood next to the cambium or sometimes vaguely in the growth of the preceding spring. Elsewhere it absorbed only

the safranin. In transverse and longitudinal sections of both stem and root of the seedling it is typically uniform in thickness throughout the pit. Fig. 43 shows this condition in the stem; Fig. 44 in the root. Sometimes, near the cambium, as in the young root of the adult, a delicate thickening produces, in sections, a flat spindle.

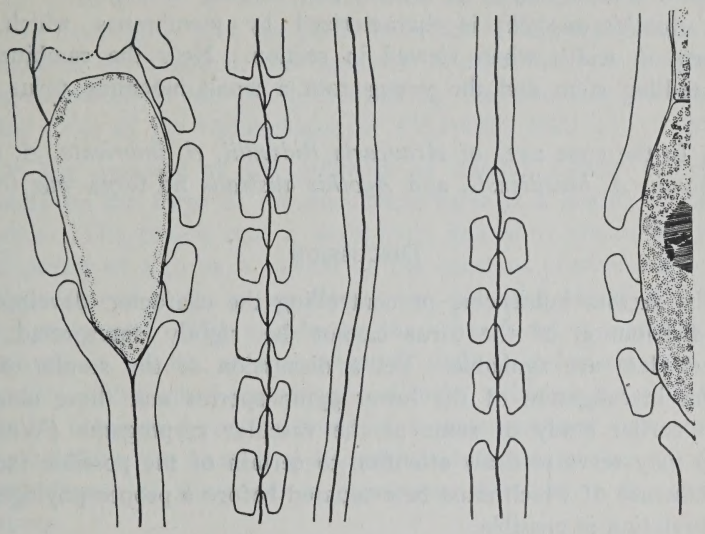

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Fig. 43. *Agathis australis.* Tangential section of the seedling stem. x 1250.
Fig. 44. *Agathis australis.* Tangential section of the seedling root. x 1250.

Summary of the Araucarians

1. The typical pitting in the stem of the araucarians studied is uniseriate and alternately biseriate. The pits are round or oval with broad borders and oval pores. In the root and cone axis there is a marked tendency toward a multi-seriate condition. Flattening of the pit margins may occur where the pits are crowded.

2. The pit-closing membrane throughout the araucarians is extremely variable. It may be either thick or thin over its whole extent or may develop centrally a more or less definite thickening. All these conditions are to be found within the radius of a single section through a given region. The behaviour of the membrane toward the stains ordinarily used for wood is variable also.

3. In *Araucaria Bidwillii* a membrane uniform in thickness is found throughout the regions studied. In the stem this is supplemented by a torus spindle-shaped in section.

4. *Araucaria imbricata* also exhibits an unmodified membrane throughout. In addition there is found in the stem, old root, and seedling stem near the cambium a torus similar to that of *Araucaria Bidwillii,* spindle-shaped in section and varying in length.

5. *Agathis australis* is characterized by membranes which are uniform in width when viewed in section. Near the cambium of the seedling stem and the young root a small indefinite torus may occur.

6. In the cone axes of *Araucaria Bidwillii, A. imbricata, A. Cunninghamii, A. brasiliensis,* and *Agathis australis* no torus was found.

Discussion

The factors influencing or controlling the character, development and distribution of the torus cannot be rightly interpreted until further data are available. Yet a discussion of the results of the present investigation of the lower gymnosperms and those obtained in an earlier study of some of the vascular cryptogams (Wright, 1920) may serve to draw attention to certain of the possible factors, the influence of which must be evaluated before a proper phylogenetic interpretation is possible.

There is, doubtless, concerned in the production of the torus a complex of causal agents. These may be of a physiological or an ecological nature, such as the action of the torus, the evaporating surface of the plant, its height, or its inhabitat—particularly as regards available moisture. Or, again, they may be morphological. The structure of the wood elements themselves, the sculpturing of their walls, the form and proportions of the pits in which the membrane occurs may be not only correlated with but possibly responsible for the thickening of its central area.

The rôle played by the torus in the physiology of the plant has not yet been satisfactorily determined. Dixon's (1914) gas-valve hypothesis put forward in connection with his cohesion theory of the ascent of sap has been questioned by Bailey (1916) while Scarth (1928), in a preliminary note of a forthcoming paper, now claims evidence in support of Dixon's view. Further work on the function of the torus is very desirable and may throw valuable light on the problem of its origin. Equally valuable would be a detailed com-

parison of the amount of transpiration relative to the sectional area of the vascular tissue in a number of forms in which the nature of the pit-closing membrane is known.

With regard to the other factors already suggested, height in plants as a dominating one, may, I think, be definitely ruled out. While the cycads, in which only an unthickened membrane develops, are all small plants in comparison with the araucarians in which a torus is developing, and the pines in which it has reached its most pronounced development, this apparent relation between height and torus formation is entirely discredited by the discovery of the substantial torus of the Ophioglossaceae (WRIGHT, 1920).

On the question of the influence of habitat (water content of the soil) on the form of the membrane there is a dearth of definite evidence. The theory that a xerophytic habitat is conducive to the development of a torus is upheld by the constant presence of a well-developed torus in the genus *Pinus,* for example, which is a highly xerophytic group. The cycads, on the other hand, a group equally xerophytic in habitat, at once negative such an inference with their constantly unthickened membrane. Crucial evidence on this factor might be obtained from the study of a water-tolerant form such as *Larix* in which the torus is well-established, by comparing the degree of prominence of the torus in specimens taken from dry and wet situations.

From the evidence so far collected on the morphological side, it appears that the structure of the pit, particularly the type of pore, is closely connected with the presence or absence of a torus. As far as my work has gone the torus has been found always in wood in which the pitting is of the round or oval, broad-bordered type, and where the pores depart from the elongated, slit-like form and become broadly oval or round. Among the cryptogams only *Botrychium* and *Helminthostachys* exhibit this type of pit and pore, and here the torus is developed. None of the cycads are characterized by round pores and in none has a torus been found. *Ginkgo* and the araucarians provide further evidence of a connection between the presence of a torus and the occurrence of broad-bordered pits with round or nearly round pores. They demonstrate, however, that the presence of a round pore does not necessarily entail the development of a torus. Undoubtedly the size of the pit should also be considered, as already suggested by Jeffrey (1917), but this can be better taken into account when the higher forms have been studied.

No matter what the causal factors involved in its production, the torus like all anatomical features will have a certain phylogenetic significance. One must, of course, guard against laying too much stress upon this aspect of the question before an investigation has been made into the higher gymnosperms. Still, the results so far obtained show that in the cycads there is a constant uniformity in thickness of the pit-closing membrane. This anatomical feature they have in common with the ferns, the supposed ancestors of the group, and yet there is among the ferns an exceptional development of a torus in the Ophioglossaceae which is quite remarkable. The possibility that it is merely a relic from tree-like ancestors is not borne out by fossil evidence. It would seem probable, however, that the source of their pitting, almost abietinean in character, has been the source also of their torus. It may be that such a line of development in this group constitutes one of those anomalous forerunners of evolution which are to be found in other groups of the plant kingdom as well, such as the appearance of vessels in *Pteris* and the Gnetales. Each of these heralds seems to get lost in a blind alley in its own group while a more generalized yet ancestrally related type keeps to the highway of evolution. The occurrence in *Ginkgo* of a torus of some sort in nearly all regions except the reproductive axes indicates that the torus, although of recent origin, has become well established. In the araucarians, on the other hand, the thickened membrane seems less firmly ensconced. With one exception it is most prevalent in the regions where anatomical characters are becoming specialized, that is in the stem and old root, and occurs more sporadically in those regions which are conceded to be more ancestral in character. From the evidence available it can scarcely be doubted that in these lower Gymnosperms we find the forerunner of the specialized type of torus occurring in the higher.

This work was undertaken at the suggestion of Professor R. B. Thomson, to whom I am deeply indebted not only for material but also for valuable criticism and encouragement throughout its progress. My thanks are due also to the following who have been most generous with material and sections: Dr. A. W. Hill, Director of the Royal Botanic Gardens, Kew; Professor C. J. Chamberlain of Chicago; and Professor H. B. Sifton, Toronto.

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EXPLANATION OF PLATES

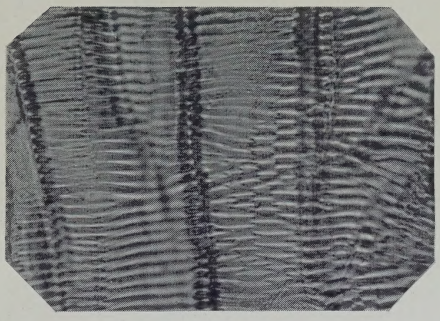
PLATE I.

Fig. 1.—*Stangeria paradoxa*—Radial section of petiole. x 400.
Fig. 2.—*Stangeria schizodon*—Radial section of the petiole. x 520.
Fig. 3.—*Dioon spinulosum*—Radial section of the stem. x 156.
Fig. 4.—*Ginkgo biloba*—Radial section of the stem. x 156.
Fig. 5.—*Agathis australis*—Radial section of the stem. x 156.

PLATE II.

Fig. 6.—*Araucaria imbricata*—Tangential section of the root. x 1000.
Fig. 7.—*Zamia integrifolia*—Section of the root. x 1000.
Fig. 8.—*Agathis australis*—Tangential section of the cone axis illustrating the uniformity of the membrane when thick. x *ca.* 1000.
Fig. 9.—*Araucaria imbricata*—Tangential section of the root showing a split torus. x 1000.
Fig. 10.—*Ginkgo biloba*—Radial section of the seedling stem showing strap-shaped torus. x 700.
Fig. 11.—*Agathis australis*—Tangential section of the cone axis illustrating the uniformity of the membrane when thin. x *ca.* 1000.
Fig. 12.—*Araucaria Bidwillii*—Tangential section of the cone axis. x 1000.
Fig. 13.—*Agathis australis*—Transverse section of the root. x *ca.* 800.

PLATE I



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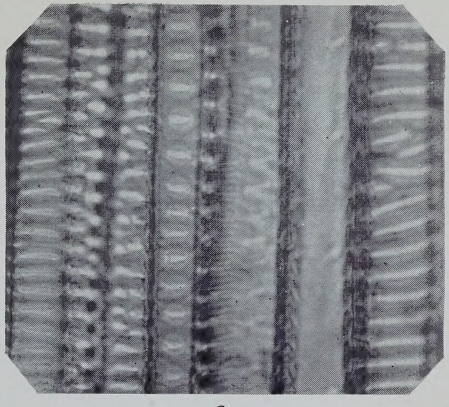

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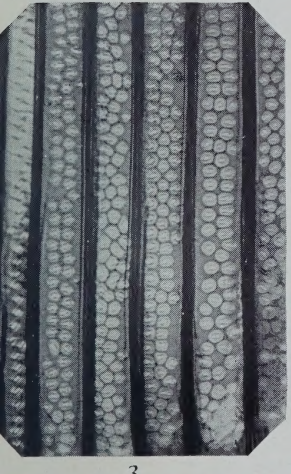

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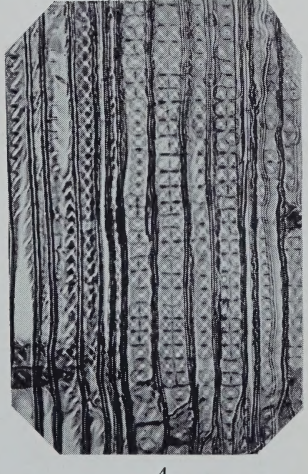

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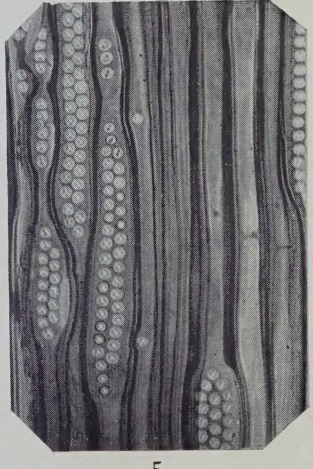

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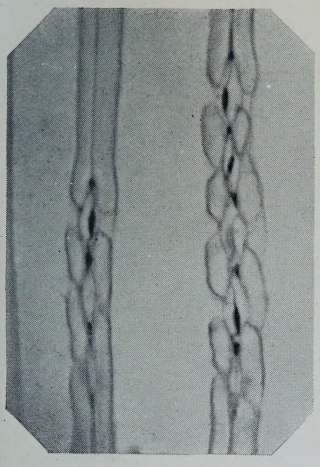

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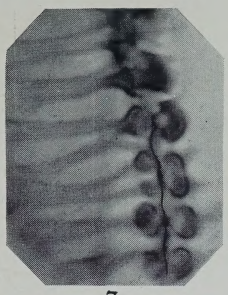

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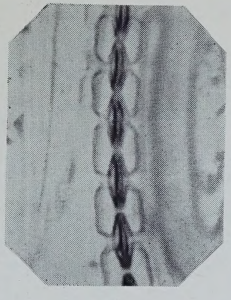

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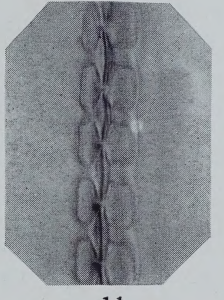

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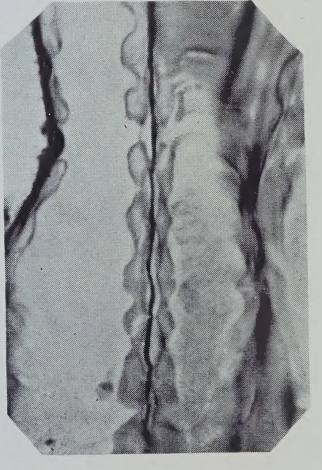

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